1   **Mediterranean Marine Heatwave 2023: Ecosystem and Fisheries impacts in Italian waters**

2   **Riccardo Martellucci R.**[1], Francesco Tiralongo F. [2],Sofia F. Darmaraki [3], Michela D'Alessandro [1], Giorgio

3   Mancinelli [4], Emanuele Mancini [4], Roberto Simonini [5], Milena Menna [1], Annunziata Pirro [1], Diego Borme [1], Rocco

4   Auriemma [1], Marco Graziano [1], Mauri Elena [1]

6   [1] National Institute of Oceanography and Applied Geophysics (Trieste, Italy)

7   [2] University of Catania (Catania, Italy)

8   [3] Foundation for Research and Technology Hellas (Heraklion, Greece)

9   [4] University of Salento (Lecce, Italy)

10   [5] University of Modena and Reggio Emilia (Modena, Italy)

11   Corresponding author: rmartellucci@ogs.it, sofia.darmaraki@dal.ca

13   **Abstract**

15   In 2023, the Mediterranean Sea experienced the longest recorded Marine Heatwave (MHW) in four decades, affecting

16   marine biodiversity, fisheries and coastal livelihoods. In this study, we assess the effects of this extreme event on the

17   proliferation of the invasive species *Callinectes sapidus* (Atlantic blue crab) and *Hermodice carunculata* (bearded

18   fireworm)*,* along Italian coasts. Focusing on the coastal area of Po River Delta in the northern Adriatic Sea and on the

19   Northern and Southern Sicily coast, we explore the possible contribution of elevated seawater temperatures in

20   increasing the monthly biomass of these species. Given that, the expansion of the Atlantic blue crab is responsible for

21   substantial economic losses in bivalve fisheries and the proliferation of bearded fireworm poses health risks to artisanal

22   fishers, we further assess the socio-economic implications of this MHW, through an analysis of fish market data and

23   online survey responses. Finally, we discuss potential mitigation strategies to manage the spread and ecological impact

24   of these invasive species, considering the aggressive feeding behavior of the former and the thermophilic nature of

25   the latter, whose venomous setae also poses health risks to humans. Overall, the sustainability of Mediterranean marine

26   ecosystems and coastal communities requires robust interdisciplinary collaboration to address the challenges posed

27   by biological invasions and climate change in the region.

28
29   **1.Introduction**

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31   The Mediterranean Sea, one of the world's most biodiverse marine ecosystems (Coll et al., 2010), is currently facing

32   unprecedented challenges due to climate change-induced extreme warm temperature events, known as marine

33   heatwaves (MHWs) (Darmaraki et al., 2019). Over the past decades, the basin has seen an increase in the frequency,

34   intensity, and duration of these record-breaking episodes, largely due to the mean warming trend of Mediterranean

35   Sea Surface Temperature (SST), ranging between 0.035-0.041 °C/year (EU Copernicus Marine Service Product,

36   2022a), nearly double the corresponding global SST trend of 0.015 ± 0.001 °C/year (EU Copernicus Marine Service

37   Product, 2022b). This has substantial implications for the region's biodiversity and economy, as the warming trend

38   and MHWs can facilitate the proliferation of invasive species (Joyce et al., 2024).

39   Among the species that pose a significant threat are the Atlantic blue crab, *Callinectes sapidus*, and the bearded

40   fireworm, *Hermodice carunculata*, which have gained attention, as a result of their rapid expansion and adverse

41   impacts on Italian fisheries (e.g., Heilskov et al., 2006, Riera et al., 2014, Simonini et al., 2019, Righi et al., 2020,

42   Bardelli et al., 2023, Tiralongo et al., 2023). In particular, *C. sapidus*, native to the Atlantic, has rapidly colonized

43   Italian coastlines (Mancinelli et al., 2021). Characterized by its voracious predatory behavior and opportunistic feeding

44   habits (Mancinelli et al., 2021), *C. sapidus* has led to substantial economic losses on bivalve fisheries and formidable

45   challenges to native species (Clavero et al., 2022). Similarly, *H. carunculata*, a thermophilic polychaete, has become

prevalent in Italian waters, adversely impacting artisanal fisheries by both ruining the catch and posing health risks to human health (Heilskov et al., 2006, Riera et al., 2014, Simonini et al. 2019, Righi et al., 2020,, Tiralongo et al., 2023). Indeed, with its venomous setae, *H. carunculata* is capable of causing painful stings to humans, with burning and erythema upon physical contact, posing health risks to tourists in coastal areas and to fishermen primarily during net cleaning (Tiralongo et al., 2023). Furthermore, *H. carunculata* represents an ecological disruptor as well as a direct threat to the well-being of coastal communities. The resilience of both species to environmental stressors and rapid population expansion highlight the urgency of addressing the compounding risks of climate change and bioinvaders with comprehensive management strategies.

The year 2023 marked a turning point, with mean global air temperatures reaching unprecedented peaks (Copernicus, 2024). The European continent encountered its second-warmest year on record, with the Mediterranean basin experiencing a series of extreme temperature events (Marullo et al., 2023). Of notable concern was the occurrence of the longest-recorded and one of the strongest surface MHWs over the past four decades, that persisted in the northwest Mediterranean from May 2022 until the boreal spring of 2023 (Marullo et al., 2023; Pirro et al., 2024 OSR8). At its peak in July 2022, this MHW covered almost the entire western Mediterranean basin, with maximum daily SST anomalies reaching about 2.6°C and 4.3°C and the anomalously warm conditions being comparable to the summer MHW of 2003 (Guinaldo et al., 2023). The long duration of the event was attributed to a combination of anomalously low wind speeds, high insolation, and weak vertical mixing in the ocean (Marullo et al., 2023). These worming related events had far-reaching effects on marine life and coastal communities (He and Silliman, 2019).

This study aims to explore the expansion and increase in abundance of *C. sapidus* and *H. carunculata* in relation to the mean and extreme warming in two coastal areas of Italy, particularly during the MHWs of 2022/2023. Relevant socio-economic implications were also assessed through the analysis of fish market data and the responses on questionnaires administered to local fishermen and completed online, which addressed issues related to the bioinvasion of these species. Furthermore, we discuss possible solutions to mitigate the invasion of these species.

2. Methods

2.1 Study areas

The study was conducted in two different regions within Italian waters: two adjacent lagoons in the Northern Adriatic Sea (Canarin and Scardovari) and two coastal areas of Sicily.

2.1.1 The Po river delta

The two lagoons under investigation in the Northern Adriatic Sea are transitional and shallow-water environments situated within the Po Delta and are connected with the sea and various river branches (Figure 1). As they are directly influenced by the Po River outflows, these regions exhibit highly dynamic hydro-morphological features and undergo rapid changes due to biotic and abiotic forces (Maicu et al., 2018; Franzoi et al., 2023). Despite facing various forms of anthropogenic pressure that have progressively altered their natural ecological characteristics (Franzoi et al., 2023), the lagoons support several clam and oyster farms, which constitute the main production activities and vital economic resources at both local and regional scales (Turolla et al., 2008; Donati & Fabbro, 2010; Bordignon et al., 2020, Chiesa et al., 2025, Tiralongo et al. 2025). The Scardovari Lagoon spans an area of 32 km², has an average depth of 1.5 meters (Mistri et al., 2018), and is connected to the sea via two inlets located at the northeast and southwest of the basin. The Canarin Lagoon covers an area of about 6.4 km² in the southern part of the study area, with an average depth of 0.9 meters (Figure 1). It is connected to the Adriatic Sea through a shallow, approximately 200-meter-wide mouth with a maximum depth of 2.5 meters.

2.1.2 Sicily

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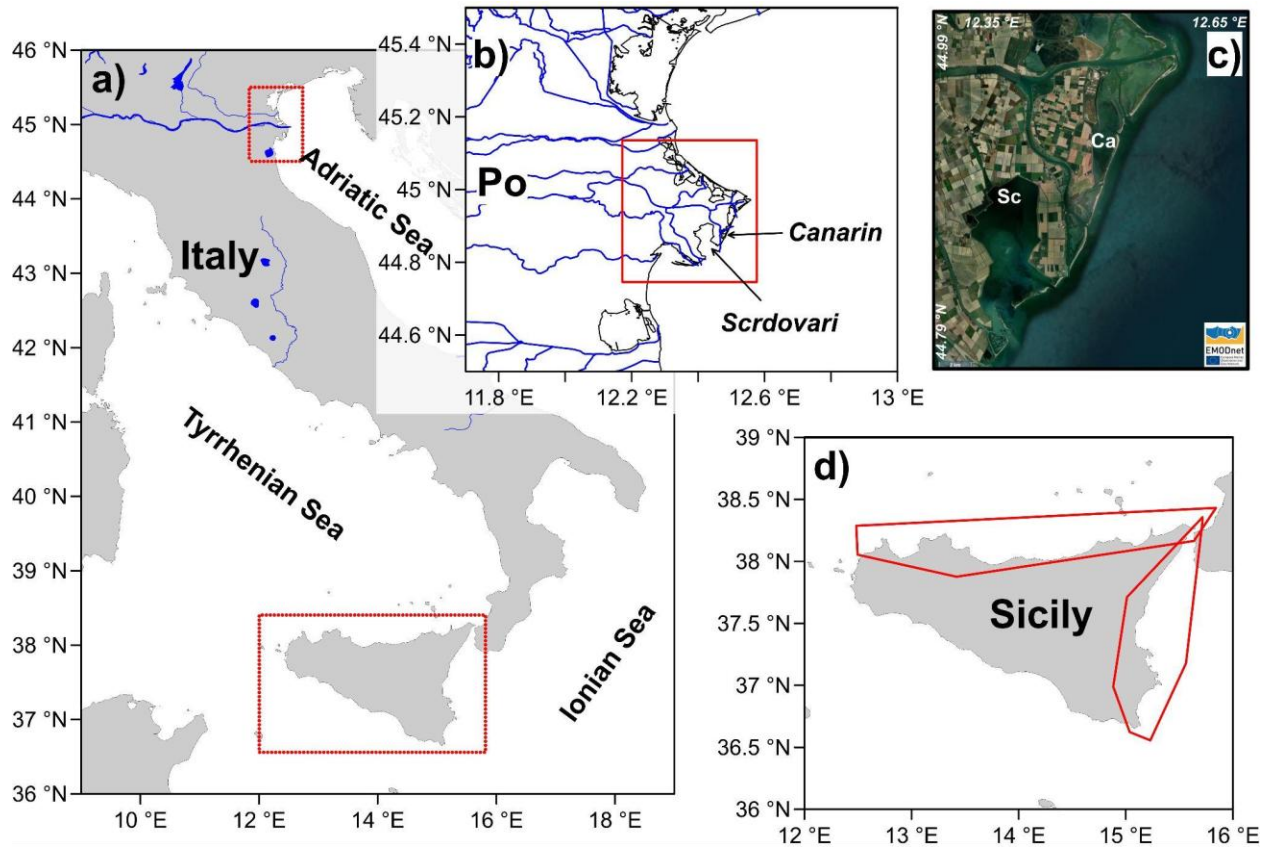


Figure 1: *Map of Italy (a) with the two study areas highlighted in red boxes. The map shows the main water basins in the region, with blue line indicating 10m Rivers and Lakes Centerlines. (Retrieved from https://www.naturalearthdata.com). The Po river delta (b) and a detailed enlargement of the Scardovari (Sc) and Canarin (Ca) are highlighted in Panel C, downloaded from the EMODnet. Digital Bathymetry available at: https://portal.emodnet-bathymetry.eu/. The examined study (coastal) areas in Sicily island (d). For images of C. sapidus and H. carunculata, refer to Figures S4 and S5.*

Sicily Island is situated at the convergence of the eastern and western basins of the Mediterranean Sea, influenced by both the relatively cooler Atlantic waters and the warmer Levantine waters (Figure 1). Specifically, the eastern coast of Sicily (Ionian Sea) is significantly affected by quasi-decadal reversals of the Northern Ionian Gyre, driven by the mechanisms of the Bimodal Oscillating System in the Ionian Sea (Gačić et al., 2021; Menna et al., 2022). The distribution of water masses is altered by bringing warm and salty Levantine water during the cyclonic phase (counterclockwise) and transporting cooler Atlantic waters during the anticyclonic phase (clockwise). This dynamic influences marine ecosystems, favoring the presence of Levantine species during the cyclonic phase and vice versa (Civitarese et al., 2023). In comparison, the northern coast of Sicily (Tyrrhenian Sea) experiences less salty and relatively cooler Atlantic waters entering through the Sardinia Channel (Vetrano et al., 2010), while the southern coast of Sicily is characterized by cold waters due to a semi-permanent upwelling (Raffa et al., 2017).

2.2 Biological characteristics of the two species

2.2.1 *Callinectes sapidus*

The Atlantic blue crab *C. sapidus* Rathbun, 1896 is a species native from the western coasts of the Atlantic Ocean, naturally distributed from Nova Scotia to northern Argentina (Millikin and Williams, 1984). It was first recorded in Europe in 1901 and in the Mediterranean since 1947 (Mancinelli et al. 2021). The first record in Italian waters dates back to 1949 in the Venice Lagoon and ballast water is considered the most likely reason (Nehring, 2011). In

Mediterranean waters, *C. sapidus* is recognized as one of the top 100 most invasive alien species (Zenetos et al., 2005; Katsanevakis et al., 2018; Tsirintanis et al., 2022) and is present in at least seven of the nine South-European Marine Ecoregion (Mancinelli et al., 2017a,b). Over the last decade, **it** has rapidly expanded its range in new ecosystems throughout the Mediterranean, such as the European Atlantic waters of Portugal, France, Belgium and Germany, but also in Italian waters (Tiralongo et al., 2021; Bardelli et al., 2023). This eurythermal and euryhaline species is a voracious predator characterized by aggressive behavior, high fecundity, excellent swimming ability and high fertility (Tsirintanis et al., 2022), inhabiting lagoons, estuaries and other coastal environments. *C. sapidus* have a complex, biphasic life cycle consisting of marine planktonic larvae (zoea) followed by benthic post larvae (megalopa), with juveniles and adults residing in estuaries, lagoons, and other coastal habitats (Lipcius et al., 2007). In marine waters, this species lives mainly on soft substrates between 1 and 90 m deep. Its life cycle is very complex and involves different environments depending on sex and ontogenetic stage: adults can reach a relatively large size, with a carapace up to 25 cm wide in males and 18 cm in females (Millikin and Williams, 1984), and reside in lagoons and estuaries where males tend to settle and molt. After copulation, oviparous females move to the sea where they lay their eggs; juveniles return to transitional environments and, after rapid growth, reach maturity in the second year of life (Millikin and Williams, 1984; Taylor et al., 2021). *C. sapidus* exhibits opportunistic feeding behavior, primarily preying on fish and invertebrates, especially bivalves and polychaetas, and can consume detritus and macrophytes when other food sources are scarce (Mancinelli et al., 2017; Tiralongo et al., 2024). Recent studies conducted in the Po delta revealed that *C. sapidus* significantly affected the aquaculture of *Ruditapes philippinarum* (Manila clam). Predation by *C. sapidus* resulted in clam losses of up to 100% in certain areas, with up to 56% of clam shells showing signs of predation and a complete absence of seeds in natural recruitment zones (Azzurro et al., 2025; Chiesa et al., 2025; Tiralongo et al., 2025). Although several studies have been carried out on this species, the impacts/interactions of *C. sapidus* on native species and Mediterranean aquatic ecosystems are still poorly understood and require further investigation (Mancinelli et al. 2017; Clavero et al. 2022).

2.2.2 *Hermodice carunculata*

The thermophilic amphinomid *H. carunculata* (Pallas, 1766), commonly known as bearded fireworm, is a large predator/scavenger polychaeta, present in warm and temperate areas of the Caribbean Sea, Atlantic Ocean, Red Sea (Fishelson, 1971; Ahrens et al., 2013; Ramos & Schizas, 2023) and the Mediterranean, (Baird, 1868, Simonini et al., 2018; Toso et al., 2022, 2024). Despite native to the Mediterranean, it is also considered as a highly invasive species, due to its increasing expansion. Previous studies point out an increase in its abundance throughout the Mediterranean basin in recent years, likely due to warmer temperatures, which favor its northward expansion (Righi et al., 2020; Toso et al., 2022). This may lead to detrimental effects on the region's ecosystems and associated species, as well as on human health, as it is resilient to natural and anthropogenic stressors (Schulze et al., 2017) and may also become a carrier of new pathogens (Sussman et al., 2003; Schulze et al., 2017). Similarly, coastal and anthropic activities, such as fishing (Figure S5) and bathing may be also affected (Celona & Comparetto, 2010; Cosentino & Giacobbe, 2011; Schulze et al., 2017; Simonini et al., 2018; Righi et al., 2020; Toso et al., 2020; Tiralongo et al., 2023). *H. carunculata* can exceed 70 cm in length and can reach 9 years of lifespan (Simonini & Ferri, 2022). Its metameres are equipped with dorsal calcareous chaetae, which are filled with a toxin that is highly effective against predation (Kicklighter and Hay, 2006; Schulze et al., 2017; Simonini et al., 2018, 2021; Righi et al., 2021, 2022). The presence of these defensive mechanisms makes the polychaete highly resilient to predation, with no identified species in the Mediterranean capable of effectively preying upon it (Ladd & Shantz 2016; Righi et al., 2021; Simonini et al., 2021). On the contrary, *H. carunculata* acts as a voracious predator of sessile and benthic invertebrates (Wolf and Nugues 2013; Wolf et al., 2014; Jumars et al., 2015; Barroso et al., 2016, Schulze et al., 2017; Simonini et al., 2018; Righi et al., 2020), and its ability to regenerate, promotes its expansion (Toso et al., 2024). Furthermore, this species is distinguished by a remarkable dispersal capacity, which is attributed to the production of planktotrophic and particularly long-lived larvae (Ahrens et al., 2013; Shulze et al., 2017; Toso et al., 2020). In Italian waters, *H. carunculata* is common and abundant on rocky substrates between 1 and 20 m (Righi et al., 2020; Simonini et al., 2021), but in some areas of the

Mediterranean it reaches greater depths and has also been observed in association with coralligenous and pre-coralligenous bio-formations (Fishelson 1971; Righi et al., 2020).

Table 1: Products used in the present work. Complete references for the articles in Prod. 1, Prod. 3 and Prod. 6 are reported in the bibliography.

Ref. no.	Product name & type	Documentation
Copernicus products		
1	Copernicus Marine SST_MED_SST_L4_REP_OBSERVATIONS_010_021 Mediterranean Sea - High Resolution L4 Sea Surface Temperature Reprocessed	Merchant et al., (2019) https://doi.org/10.48670/moi-00173
2	Copernicus Marine MEDSEA_MULTIYEAR_PHY_006_004_E3R1 Mediterranean Sea Physics reanalysis	Escudier et al., (2021) Dataset: Escudier et al., (2020) https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1
Non Copernicus products		
3	Crab and clam fishery data	CONSORZIO COOPERATIVE PESCATORI DEL POLESINE Organizzazione di Produttori Soc. Coop. A r.l., Via della Sacca, 11 45018 Scardovari (RO) – ITALIA. P.IVA 00224140293
4	Questionnaire Worms Out	Link: bit.ly/3L3TWUc https://www.facebook.com/MonitoraggioVermocane
5	Questionnaire Righi et al. 2020	https://doi.org/10.12681/mms.23117 ,
6	iNaturalist	https://www.inaturalist.org/

163   *2.3 Temperature Datasets*
164   To identify surface MHWs on the study areas we obtained daily SST data from the Mediterranean Sea SST Analysis
165   L4 product of the Copernicus Marine Service, covering the period 1982-2023 (Table 1, product ref. 1). This dataset
166   provides gap-free, optimally-interpolated, satellite-based estimates of SST, with a resolution of 0.05°x0.05°. For the
167   analysis of subsurface temperatures in the areas of interest, daily vertical profiles of temperatures were obtained from
168   the Mediterranean Sea Physics Reanalysis dataset spanning the period 1993-2023 (Table 1, product ref. 2), with a
169   spatial resolution of $0.042° \times 0.042°$. MHWs are detected whenever SSTs exceed a daily, 40-year (1982-2023)
170   climatological threshold for at least 5 days in a row, based on the identification framework proposed by Hobday et al.
171   (2016).
172
173   2.4 The crab and clam fishery data
174   To assess the impact of *C. sapidus* spread on the local fishing industry, we use data on Manila clam production,
175   provided by the Scardovari and Canarin Cooperative, which have farmed this species in the Po delta for years. The
176   dataset includes monthly values of waste and sales of *C. sapidus*, representing the sum of the fishermen's daily harvests
177   before they reach the market for fish sales (Table 1, ref. 3). Recent studies in the area have shown that *C. sapidus*
178   preys on bivalve mollusks, as evidenced by claw marks on shells. Compared to previous years, mussel (Manila clam)
179   production in 2023 declined by 75 % in the Scardovari lagoon and 100 % in the Canarin lagoon (Azzurro et al., 2025;
180   Chiesa et al., 2025, Tiralongo et al., 2025), for these reason we take the discard data as proxy of *C. sapidus* biomass
181   and damage on fisheries.
182
183   2.5 Questionnaire for *Hermodice carunculata*
184   Over the last decades, citizen participation in data collection useful for science has increased, thanks to numerous
185   awareness-raising initiatives (Turrini et al. 2018) and has already been recognized as a valuable resource for research,
186   biodiversity monitoring, and conservation (Lopez et al., 2019; Toivonen et al., 2019). While, in some cases, this
187   information lacks a solid scientific basis, requiring validation by experts in the field, it offers the advantage of being
188   gathered over broad geographical areas at a low cost (Ballard et al., 2017; Tirelli et al., 2021; Sun et al., 2021). For
189   this reason, citizen science projects are currently increasing in several fields, especially as a tool to address
190   environmental and conservation issues (Kullenberg et al., 2016; Turrini et al., 2018). For instance, citizen involvement
191   is widely used in projects and initiatives related to the sighting of non-indigenous species, invasive and uncommon
192   species, such as AlienFish project (https://www.facebook.com/alienfish), avvistAPP (https://www.avvistapp.it/),
193   Monitoraggio Vermocane (https://www.facebook.com/MonitoraggioVermocane) and ìNaturalist
194   (https://www.inaturalist.org/).
195   To assess the impact of *H. carunculata* on human activities, such as fishing and tourism, a questionnaire was developed
196   and administered to fishermen and distributed as an online survey. The questionnaire built upon the observations by
197   Righi et al. (2020) was administered in 2023 to a diverse group of individuals, yielding a total of 151 responses.
198   Distributed primarily through websites, such as the "Monitoraggio del Vermocane", and the "Fauna Marina
199   Mediterranea" (https://www.facebook.com/groups/230601830399549) and via social media pages of various authors,
200   it was also shared with Italian scuba diving centers. The questionnaire comprised 19 questions, of which four single-
201   choice questions, focusing on the frequency of sightings, the abundance of specimens, and perceptions of the species
202   as a potential issue, were analyzed in this study. Most respondents reported observing the fireworm during scuba
203   diving (74%), spearfishing (10%), and snorkeling (15%) activities, while no questions about the respondents' age or
204   employment status were included. Due to its distinct morphology and vibrant coloration, *H. carunculata* is unlikely
205   to be mistaken for other species, as no comparable organisms exist in the Mediterranean. This survey was conducted
206   as part of the Worms Out project, funded by the National Institute of Oceanography and Applied Geophysics and the
207   ECCSEL NatLab Italy project (Table 1, ref. 5). In addition to real-time data collected from maritime users, the use of
208   this questionnaire is important for identifying and assessing the presence of this species, addressing the current lack
209   of scientific reports on the species, likely due to sampling limitations (e.g., Fraschetti et al., 2002; Giangrande et al.,
210   2003; Corriero et al., 2004; Mastrototaro et al., 2010). To address the scarcity of scientific reports, we integrated
211   observations from different sources such as the ìNaturalist observations, findings of Righi et al. (2020) and recent

 Integrating this information with scientific literature and observations, is crucial for monitoring biological invasions and studying native invader species (Azzurro et al., 2019; Giovos et al., 2019; Toivonen et al., 2019).

3. Results

3.1 Northern Adriatic

During the first half of 2023, clam production in the area was about 400 tons per month, reaching a production peak in August (800 tons), before drastically declining from September through December (Figure 2a). In contrast, crab sales began during the summer months, with the highest discard observed in August 2023, totalling 300 tons. Towards the end of 2023, crab discard levels were comparable to sales (Figure 2b). Throughout 2023, the North Adriatic study area was also characterized by particularly high SSTs with six MHWs observed (Figure 2c and d). The first event occurred during March, lasted for 5 days and had a moderate intensity, while the rest of the events occurred during the summer and autumn season. The most intense MHW was observed at the end of August 2023, characterized by temperatures over 3°C higher than normal and 11 days duration (Table S1). The longest event was observed in October, persisting for 36 days with a strong intensity (>2.6°C). The high temperatures of 2023 affected the entire water column as well, with the most intense subsurface temperature anomalies (>4°C) seen between 4m and 15m depth during the summer season (Figure 2d). This indicates a significant rise in subsurface temperatures in the area, given that typical deviations from the 1993-2016 mean range between 0.8°C and 1.2°C (Figure S1). Regarding the potential cumulative temperature effects on *C. sapidus* life cycle, while the SST during 2023 has not been below the winter dormancy threshold (5°C), it has exceeded the reproductive activity (10.8°C) and larval development (19°C) temperatures, by 300 and 170 days, respectively (dashed lines in Figure 2c).

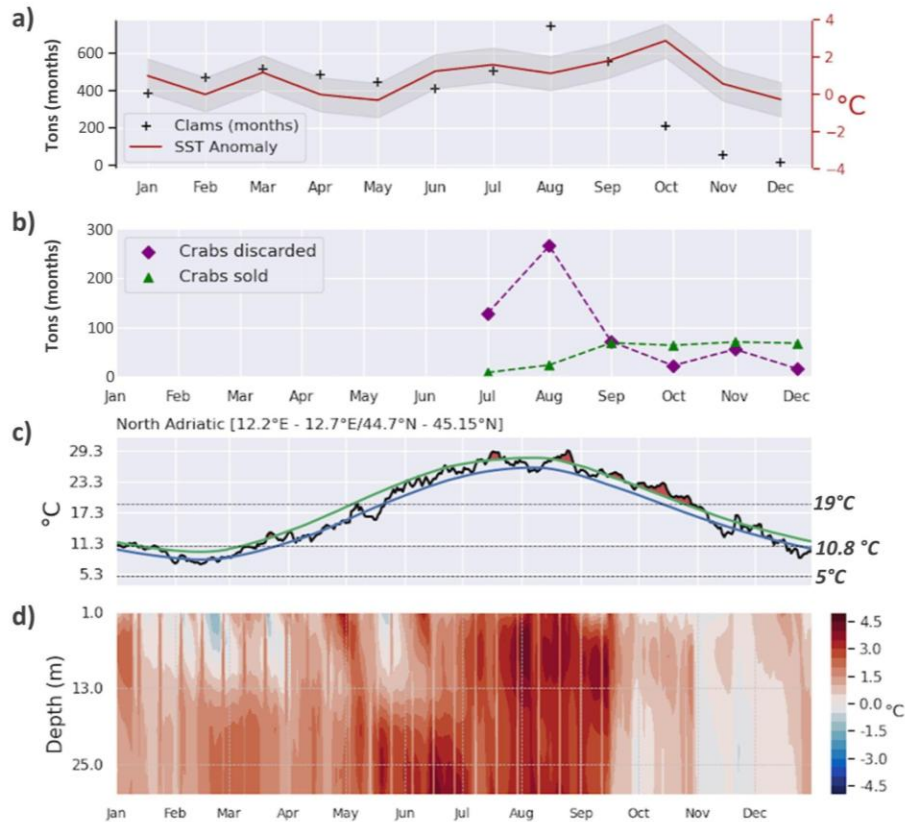
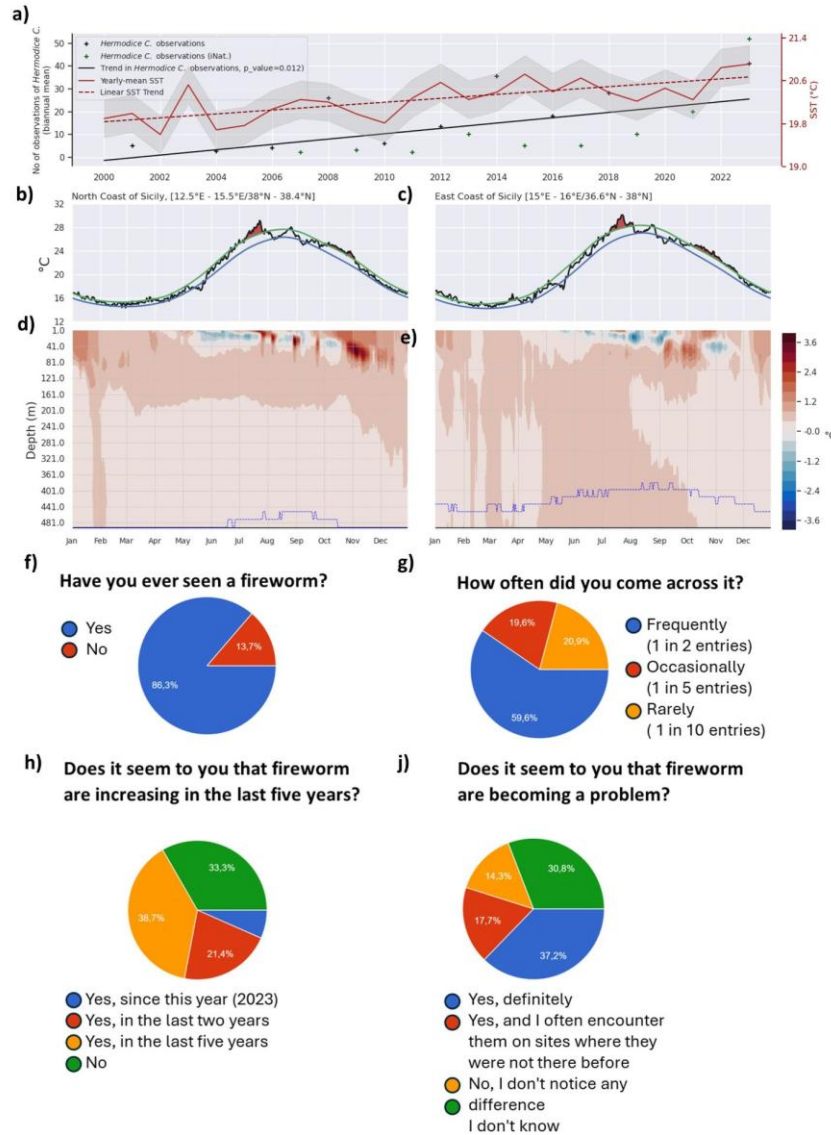



Figure 2: *Northern Adriatic study area: a) Time series of daily, spatially-averaged SST anomalies of 2023 relative to the period 1993-2016 (red line), and monthly evolution of sold clams (black cross). b) Monthly evolution of sold (green triangles) and discharged (purple diamonds) C. sapidus during 2023. c) Time series of daily, spatially-averaged SST during 2023 (black), smoothed SST climatology (blue) and 90th percentile threshold of SST (green) based on the 1982-2023 period. MHWs are indicated in red and identified using the Hobday et al. (2016) definition. The three dashed lines represent the temperature thresholds for winter dormancy (5°C), reproductive activity (10.8°C) and larval development (19°C) of C. sapidus. d) Vertical profile of temperature anomalies during 2023, relative to the period 1993-2016, spatially-averaged at each depth. Temperature data were obtained from Copernicus Marine Service (Table 1, product ref. 1, 2), Clams and Crab data were obtained from the Consorzio Cooperative Pescatori del Polesine (Table 1, product ref. 3)*

3.2 Sicily

In the two coastal regions of northern and eastern Sicily SST remained above climatological values throughout 2023 (Figure 3b,c): Eastern Sicily experienced three MHWs that lasted approximately 60 days in total (Table S1). The most intense event occurred in July, persisting for 21 days and the longest one during October, lasting for 30 days. On average, the northern coast of Sicily, experienced slightly longer MHWs: The first event occurred in March, lasted for 5 days and had an intensity of 1.4°C. The most intense MHW (>2.5°C) was observed between July-August, lasting for 25 days, while the longest event (49 days) occurred during autumn with an intensity of 1.6°C. Relative to the 1993-2016 period, temperatures throughout the water column in both regions were warmer than normal, by approximately $1.2°C$ - $4°C$, and more so in the northern coast of Sicily. The upper 80 meters of the water column exhibit the highest temperature anomalies (>2°C) throughout the year, especially during autumn months (>2.5 °C) in both areas. However, during some days of the summer period, subsurface layers between 10 and 50 meters depth exhibit negative (up to -2 °C) temperature anomalies (Figure 3d,e), with temperatures dropping below 14 degrees only at greater depths. Typically, subsurface temperatures deviate approximately 0.8 - 2°C from the 1993-2016 mean, with the highest values observed in the upper 20-80 m depth between June-November (Figure S1). The progressive temperature increase of around 0.03 °C/year observed along the Northern coast of Sicily appears to correspond with a rising trend in *Hermodice carunculata* records over the last 20 years, predominantly during 2007-2008, 2014-2015 and 2023, when

257 the highest number of observations were recorded (Figure 3a). This increasing trend is also supported by the results
258 of our proposed questionnaire, revealing a significant increase in the frequency of sightings in recent years compared
259 to 2018, particularly during recreational activities. Specifically, the results of the questionnaire demonstrate that the
260 presence of this species is increasingly recognised as a growing issue, particularly as *H. carunculata* is observed in

261 areas where it has not been seen before (Figure 3 h and j).

262 **The data from Hermodice questionnaire were compared with those obtained from the iNaturalist (Table 1, ref.**
263 **6) platform, and the two datasets showed similar observations, particularly in terms of the observed trend**
264 **(Figure 2a).**

265 ***Figure 3:*** *a) Yearly-averaged time series and linear trend of SST (red), spatially-averaged over the Northern coast of*
266 *Sicily and yearly records of H. carunculata (black cross) with their linear trend, based on Righi et al. (2019) and our*
267 *questionnaire for the period 2000-2023 (Table 1, product ref. 4 and 5), the green cross represent the biannual mean*
268 *of H. carunculata from iNaturalist. Daily and spatially-averaged SST time series during 2023 (black), smoothed SST*
269 *climatology (blue) and 90th percentile threshold of SST (green) based on the 1982-2023 period, for the Northern (b)*

and Eastern (c) coast of Sicily. MHW are indicated in red and identified using the Hobday et al. (2016) definition. Vertical profile of spatially-averaged temperature anomalies during 2023, relative to the climatological period of 1993-2016 for the Northern (d) and Eastern (e) coast of Sicily. The climatological depth of 14 °C isotherm is displayed in blue dashed line whereas the depth of the 14 °C isotherm during 2023 in solid black. d) Main results of the Worms out questionnaire (Table 1, product ref. 4). Temperature data were obtained from Copernicus Marine Service (Table 1, product ref. 1, 2).

4. Discussion and conclusions

The two study areas of the Mediterranean Sea experienced multiple, prolonged and strong surface MHWs throughout 2023, with temperature anomalies during the events ranging between 1.6°C - 2.6 °C in the East and North coasts of Sicily and between 2 - 3 °C in the Northern Adriatic coast. These events are associated with a general warming tendency, indicated by elevated monthly temperature anomalies, almost throughout the year (especially during the summer) in the Northern Adriatic and by a 0.03 °C/year trend particularly evident in the SST along the coast of Northern Sicily for the period 2000-2023. Compared to the study areas in Sicily, the Northern Adriatic exhibited a slightly stronger warming throughout the water column, likely due to its shallower depth. However, lower than normal subsurface temperatures were observed in the upper 40 m of the two study areas in Sicily, during certain periods in summer and autumn. This feature is likely associated with a stronger upper ocean stratification during those periods and a displacement of the thermocline (see Figure S2,S3), resulting in cooler temperatures nearer to the surface, similar to Pirro et al. (2024). Overall, significant warming was observed in all study areas during 2023, which may have led to an increased abundance of the two invasive species in both areas.

In the case of *C. sapidus*, higher temperatures have likely triggered a positive feedback in the phenology of larval and adult *C. sapidus*, ultimately leading to higher survival and reproduction rates and driving its population surge. A similar mechanism has been proposed for other invasive crabs, such as *Hemigrapsus takanoi* (van den Brink et al., 2012). In this context, rising temperatures may have enhanced the species' invasiveness in regions where it was previously established but remained in low numbers, as observed in the Po River estuary. Considering that winter dormancy, adult reproduction and early life stages (egg maturation, zoea and megalopa development) are strongly regulated by temperature minima (Schneider et al., 2024; Brylawsky and Miller 2006; Rogers et al., 2022), elevated temperatures may have additionally accelerated metamorphosis from zoea to megalopa, reducing predation risk and promoting the species' survival. Also for *H. carunculata* high temperatures accelerates their growth phases (Libralato et al., 2015, Alter et al., 2024) and numerous studies suggest water temperature as a key driver of its proliferation (Righi et al., 2020, Tiralongo et al., 2023, Toso et al., 2024), by influencing the species range shifts and facilitating its establishment and dispersion (Stachowicz et al., 2002; Samperio-Ramos et al., 2015). The responses from our questionnaire, as well as ìNaturalist observations, further support this expansion, revealing a notable rise in sightings over the past five years. Our results are thus consistent with the documented increases in the species' presence and its bathymetric expansion over the past two decades, coinciding with a general rise in coastal water temperatures in Sicily (Pisano et al., 2020; Righi et al., 2020, Tiralongo et al., 2023; Kubin et al., 2024), which became particularly evident during 2023 (Figure 3a). Given the ongoing warming trend in the Mediterranean Sea, this thermophilic species is likely to continue expanding along the northwestern Mediterranean coast (Righi et al. 2020), where it is frequently observed in shallow waters through the years, especially during the summer months (Schulze et al., 2017; Encarnação et al., 2019).

Overall, global warming and biological invasions in marine ecosystems are interconnected, although the extent of their interactions and the role of climate change as a driver remain a subject of debate. The impacts of climate change and biological invasions differ throughout the invasion process and are influenced by species-specific responses to warming (Katsanevakis et al., 2014, Joyce et al., 2024). These responses affect the distribution, demographics, and life histories of invasive species. For marine invertebrates with intricate life cycles, the effects of climate warming are particularly pronounced during critical stages (Libralato et al., 2015, Alter et al., 2024) such as larval development, reproductive activity, or winter dormancy (dashed line in Figure 2c). Additionally, Simonini et al. (2021) suggest that fishing practices can facilitate the dispersion, establishment and survival of *H. carunculata*, for example, by providing

317 ample food resources, during discarding fish and cleaning nets after fishing in coastal areas. Furthermore, releasing
318 egg-filled *C. sapidus* females into lagoons (where they cannot be sold on the market, as they don't seem appetizing,
319 Figure S4) can significantly increase crab larvae population in the lagoon. These examples underscore how insufficient
320 management practices can unintentionally enhance the spread of invasive species.
321 This notable increase in the monthly biomass of the *C. sapidus* in the Northern Adriatic and the annual records of the
322 *H. carunculata* along the coasts of Sicily can have various implications. Specifically, we show that the proliferation
323 of *C. sapidus* in the Po river delta has significantly disrupted clam production in 2023 (Figure S4) and under current
324 conditions, no resurgence of clams populations is expected in 2024. The damage to the clam industry is further
325 exacerbated by the costs of removing crabs discarded by fisheries (Figure S4). This expansion is anticipated to also
326 disrupt benthic habitats, alter community composition and affect the abundance of other species, similar to the impacts
327 observed with other annelids (e.g., Berke et al., 2010; Pires et al., 2015). Similarly, *H. carunculata* poses a threat to
328 both marine biodiversity and the economic stability of local fisheries. Although comprehensive documentation of its
329 effects has only recently emerged (Tiralongo et al., 2023), the species are known to inflict both direct and indirect
330 damage to fishing operations (Figure S5). Direct damage includes severing secondary lines attached to hooks, either
331 through the worm's teeth or by concealing itself among rocks after consuming the bait (Tiralongo et al., 2023). To
332 minimize these effects on target species, fishermen reduce gear soaking time, resulting in decreased catch rates
333 (Simonini et al., 2021; Tiralongo, 2020). Aside from impeding fishing efficiency, the scavenging activities of *H.*
334 *carunculata*, further impact the fishing industry by damaging fish catches and reducing the market value of affected
335 fish. The economic impact is estimated at approximately 7.32 euros per kilogram of damaged fish, resulting in
336 substantial annual losses given the total weight of commercially valuable catches (Tiralongo et al., 2023). The ongoing
337 temperature-driven expansion of *H. carunculata*, as observed in our results and documented by Righi et al. (2020) and
338 Tiralongo et al. (2023), underscores the urgent need for effective mitigation strategies to address the climate change-
339 induced impacts on fisheries, tourism and coastal economies.

Implication for human life and solutions for stakeholder

341 Although rising temperatures favor the spread of invasive species at the expense of marine biodiversity, the ongoing
342 *C. sapidus* invasion presents an opportunity to evaluate strategies and measures to contain this dispersion and mitigate
343 ecological impacts. As their economic value has already been recognized internationally, this species can be exploited
344 for both food and non-food uses. Several studies have demonstrated that overharvesting plays an important role in the
345 control of invasive species (Mancinelli et al., 2017), as exemplified by the commercial harvest of *C. sapidus*, which
346 supports a major fishery along the coasts of US (Hines, 2007, Kennedy et al., 2007; Bunnell et al., 2010); accordingly,
347 control policies should aim at similar marketing strategies. Despite its introduction to the Italian market, *C. sapidus* is
348 not yet widely consumed, complicating efforts to eradicate it. Effective management strategies should therefore
349 include cultural incorporation of this species. For example, the Italian government has promoted *C. sapidus* by
350 presenting it at the 2024 G7 summit and by disseminating promotional online content. Expanding public outreach
351 through targeted events and education campaigns could further boost its consumption, akin to successful models used
352 for other species. Additionally, the extraction of chitosan and astaxanthin from crab shells may support the ongoing
353 shellfish market, while providing valuable compounds with diverse applications in pharmaceutical, biomedical,
354 cosmetic, agricultural, and biotechnological fields (Ambati et al., 2014; see also Demir et al., 2016, Baron et al., 2017
355 for recent examples on *C. sapidus*).
356 Similarly, the increasing frequency of *H. carunculata* sightings highlights the need for effective management
357 strategies to mitigate its proliferation. As an efficient scavenger, predatory generalist and opportunistic consumer that
358 can also feed on carrions, *H. carunculata* has been also found in high abundance beneath aquaculture net cages and at
359 sites with high anthropogenic pressure and organic enrichment, such as artisanal fishery ports (Heilskov et al., 2006,
360 Riera et al., 2014; Righi et al., 2020). Due to its ability to tolerate captivity, *H. carunculata* presents potential
361 applications for the disposal of waste from the production and processing of marine products. Recent biorefinery
362 research explores its use in processing mollusk waste, specifically expired mussels from retailers, for shell recovery
363 and valorization. Preliminary findings show that *H. carunculata* consumes mussel meat at high rates, leaving the shells

almost completely clean (Simonini et al., 2024). Given its ability to maintain them at high densities without substrate, the species could prove useful for valorizing waste shells, with clean shells serving as a source of "green" calcium carbonate (Seesanong et al., 2023). Developing practical applications for this invasive species could also support removal interventions from areas where *H. carunculata* is becoming a pest (Simonini et al. 2024).

Thus, management and control costs in invaded habitats may ultimately yield profits for local populations, while the effects of the invader may be greatly reduced, even enhancing the ecosystem goods and services provided by coastal habitats. Collaborative efforts are essential for formulating adaptive measures to safeguard both marine ecosystems and the livelihoods of communities along the Mediterranean coasts. Through interdisciplinary cooperation and proactive management strategies, it is possible to mitigate the adverse effects of climate change and invasive species proliferation, ensuring the long-term sustainability of Mediterranean marine environments and the well-being of coastal communities.

Acknowledgements

Darmaraki S. acknowledge the financial support from the Hellenic Foundation for Research and Innovation (HFRI) under the 3rd Call of "Research projects to support Post-Doctoral Researchers" scheme,Project number 7077, acronym TexMed. This work was partly funded by the ECCSEL-NatLab Italy project, made by the extraordinary MIUR contribution (FOE) for the participation of Italy in the activities related to the international ECCSEL infrastructure (European Carbon Dioxide Capture and Storage Laboratory Infrastructure), with the aim of developing and maintaining of the natural laboratories of Panarea (Aeolian Islands) and Latera (Lazio).

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